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² Shannon, W. P., *Indianapolis, Proc. Acad. Sci.*, 1895, (53–54).   Moore, J., and Hole, *Ibid.*, 1902, (216–220).   Culbertson, G., *Ibid.*, 1903, (202–205).

³ Locke, J., *Ohio Geol. Surv.*, 1838, (246).   Orton, *Rep. Geol. Surv. Ohio*, **1**, 1873, (377). Perry, N. W., *Amer. Geol., Minneapolis*, **4**, 1889, (326–336).   Foerste, A., *Chicago, J. Geol. Univ. Chic.*, **3**, 1895, (50–60, 169–197).   Prosser, C. S., *Ibid.*, **24**, 1916, (456–475).

⁴ See Foerste, A., *Kentucky Geol. Surv., Bull.*, No. 7, 1906.

⁴ᵃ Dr. J. E. Hyde called my attention to this very interesting occurrence.

⁵ Foerste, A. F., *Amer. J. Sci., New Haven*, (Ser. 4), **18**, 1904, (321–342).

⁶ See Foerste's Map of the distribution of the facies of the Clinton formation.

⁷ Cornish, V., *London, Geog. J.*, **18**, 1901, (170–202).

⁸ Hunt, A. R., On the formation of ripple marks.   *Proc. Roy. Soc.*, **34**, 1882, p. 4.

⁹ L. c., p. 190.

¹⁰ Supan, A., *Grundzüge der Physischen Erdkunde*, 1911, p. 260.

¹¹ Kruemmel, O., *Handbuch der Ozeanographie*, 1911, vol. II, p. 383.   See also Berghaus, A., *Atlas der Hydrographie*, 1891, Pl. XX.

¹² To what extent inorganic or organic precipitation may have played a rôle I am in no position to judge.   Observation 7 seems to point to it as a source of finely divided calciumcarbonate.

¹³ Krümmel, O., *loc. cit.*, p. 112.

THE BEARING OF SELECTION EXPERIMENTS WITH DROSOPHILA UPON THE FREQUENCY OF GERMINAL CHANGES

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Biologists generally agree that changes in the germ plasm do occur. On the other hand, there appears to be considerable disagreement regarding the frequency of these spontaneous changes.   Some experiments, as illustrated by the work of Pearl, Hj. Nilsson, De Vries, Tower, and Johannsen,¹ are more easily analyzed by supposing that changes in the germ plasm occur very rarely in comparison with the number of generations of individuals studied, so that the origination of new races by selection is not generally possible.   Other experiments, notably those of Castle, Smith, Middleton, and Jennings (on *Difflugia*),² have been interpreted as showing that such changes are occurring so frequently that they may be found in each generation, and so afford a basis for selection to make continuous progress.   As long as different experiments lead their authors to such different conclusions, no broad generalizations as to the scope of the evolutionary significance of selection may be drawn without the most intimate and critical consideration of all other related investigations, and, accordingly, all additional evidence that may be secured has an important bearing.

The familiar Mendelian units are currently conceded to arise sud-

denly, as conspicuous changes, or mutations. But the question is not settled as to how frequently, after their appearance, further changes may occur in these units. It is upon this special phase that the results here presented have their bearing.

Most banana flies (*Drosophila ampelophila*) have four conspicuous bristles on their backs. A mutation occurred which permitted more than the normal four bristles to develop in this special region of the back. From one pair of flies produced by germ plasm bearing this mutation, an extra-bristled race was established (MacDowell)[3]. This race was distinguished from the normal wild race by one Mendelian unit, as was shown by crosses which gave first generations with no extra bristles and second generations (F_2) in which one quarter of the flies had extra bristles. The number of extra bristles in this race was variable; experiments showed that this was largely due to the amount of food eaten during the development of the flies. Large flies, those from flourishing culture bottles, had numerous extra bristles, while small flies, those from mouldy, or old, dried up cultures, had few, or even no extra bristles. But even when no extra bristles developed, these flies, when given fair breeding conditions, produced offspring all of which had extra bristles. To discover any changes in the inherited basis of this character (extra bristles), selection for increased bristle-number was carried on for 49 generations. During this time every mating was made between brothers and sisters in pairs. Considerably over 100,000 bristle-counts form the basis of the following discussion.

Two conditions must be met before selection can modify the means of a race. First there must be genetic differences between individuals, and second, these differences must be manifest to some extent in the somatic structures of the individuals. In other words there must be some tendency for extreme variates to bear extreme germ plasm. To measure this relation between soma and germ plasm, the coefficient of correlation is especially fitted. It is an expression of the degree of similarity existing between parents and offspring. All the data obtained from the inbred extra-bristled race were cast into tables correlating the grades of the parents and their offspring in each generation. The coefficients calculated from these tables show that there is an unquestionable positive correlation between the grades of the parents and offspring in the first six generations; the coefficients for these generations are statistically significant. In the subsequent generations no further evidence of any positive correlation is to be found that has biological significance. The coefficients are sometimes plus and other times minus, but without any consistency or regularity. In most cases they are not

significant in comparison with their probable errors; in some cases they are clearly significant. This means that in most cases there was no tendency for high grade parents to have higher grade offspring than low grade parents. In individual generations higher parents did produce offspring of somewhat higher grade, but then in others higher parents actually produced offspring of lower grade than did the lower grade parents. These facts indicate great independence between the grades of parents and offspring in all but the early generations; they lead one to expect to find that the selection of high variates during the early generations has modified the means of the race, but that later on the same process has failed to make further progress. What actually happened is shown in figure 1, which represents the means of the high selected race.
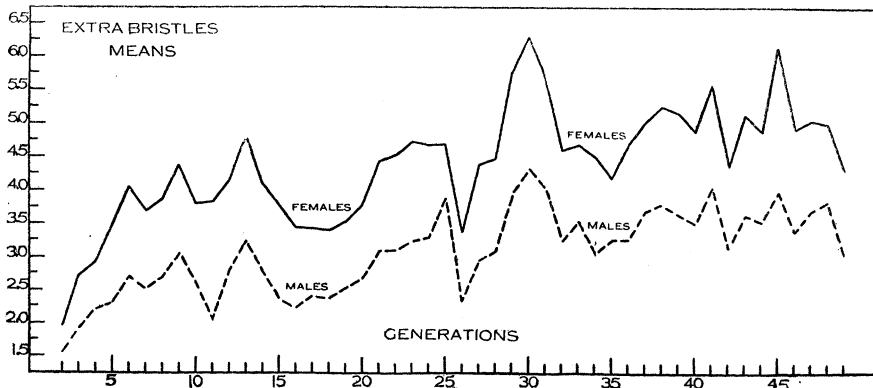

FIG. 1. MEANS OF THE OFFSPRING FROM 49 GENERATIONS OF SELECTION FOR INCREASED NUMBER OF EXTRA BRISTLES

Due to a change in method the means in generations following the 29th tend to be higher, and therefore can not be compared with the preceding ones.

The means of the males are consistently lower than those of the females, but the close parallelism of the curves serves to substantiate the correctness of the means as descriptions of the different generations. As expected, the means steadily rise for the first few generations; after this they fluctuate. It will be noted that the highest point in the curves appears in the 29th generation; this high point immediately follows the removal of the breeding bottles to a constant temperature room in which dry summer heat was automatically maintained. Moreover, due to a change in method, in the subsequent generations the means tend to be higher than those in the generation preceding the 29th. It remains, then, to compare the means before and after the 29th, separately. Where the means show regular advance, the correlation coefficients

are regularly positive and significant; where the means are irregulars and seem to depend mainly upon environment, the correlation coefficient, are irregular, plus and minus, and in general not statistically significant. It is important to understand that this failure of selection can not be explained by physical incompatibility in the soma. There is obviously plenty of room for many more bristles than are generally found and, in a few cases where very rare conditions happened to be experienced by individual flies, such extreme grades as 12, 13 and 16 extra bristles have been found, whereas the most frequent high extreme is 9 extra bristles, and the characteristic mean of the race seems to be 4.75. It may be concluded that at first there were differences in the germ plasm of the different flies and these differences were manifest in the somatic appearance, even though environment was also causing variations; later, due to the selection, such germinal differences between individuals as were clearly observed at the beginning were no longer found.

As further evidence for this conclusion the following experiment may be described, which meets the objection that the narrow range of parents selected in the later generations might account for the absence of correlation. Accordingly, selection was suspended for three generations and as far as facilities would permit, all the progeny of one pair of flies in the 50th generation were bred in pairs for three generations without respect to their grades, the only restriction being that matings were made of flies of the same or within one of the same bristle grade, and only virgin females were used. All the offspring were counted and graded. In the second generation of this experiment over 4000 flies were graded, in the third generation, 27,000.

For these generations the correlation coefficients were as follows:

Males—2d generation, $r-0.1436 \pm 0.0995$;   3d generation, $r-0.0271 \pm 0.0391$
Females—2d generation, $r-0.1378 \pm 0.0997$;   3d generation, $r-0.0221 \pm 0.0391$

This shows that the higher grade parents did not have any tendency to produce higher grade offspring than the lower grade parents, and therefore, that the failure of selection to produce further changes in the means of the race, is due to the absence of such genetic differences, as were originally present.

From quite a different source comes evidence that the early generations of selection modified the genetic constitution of the race. Starting from the second selected generation a race of low grade flies was formed in one generation by selecting low grade flies as parents. The means of this race were entirely distinct from those of the high selected race; as the high race rose, this race remained low. Since it is known

from the correlation coefficients, that the higher grade flies were pro-
ducing higher offspring at this time, it is entirely within expectation
to find that the lower grade flies could produce lower grade offspring.
On the other hand, when flies of similar low grades were selected from
the 16th generation of the high selected race, and the selection of low
grade parents continued for 8 generations as a return selection series,
the means of the offspring were not significantly lower than those of the
corresponding generations in the high selected race. In fact the suc-
cessful result of selecting low grade parents of the same grades in the
second generation was not even approximated. The correlation coeffi-
cients indicated that flies with different grades were not differentiated
genetically in the 16th generation; these breeding tests support the same
conclusion. The line from low parents started from the 16th genera-
tion, was lost after 8 generations; since low grade flies are the smaller
ones, this selection, besides separating low grade flies, isolated weak ones.
This accounts for the reduction of vigor and the final loss of the race. A
second return selection was started from the 27th generation of the high
race. For three generations the means of this line closely resembled
those of the high race, but the weakening effect was soon manifest in
the small numbers of offspring and the lowered means, and shortly, in
the loss of the race through the failure of the selected flies to reproduce.

A still further test has been made of the conclusion already stated.
If the dissimilar genetic behavior of the unselected and the long selected
flies rests on a sorting out of differences in the germ plasm, it should be
possible to bring back these differences by crosses with flies that might
be supposed to have germ plasm still bearing these differences. Flies
from the 17th generation were crossed with wild normals; from the extra-
bristled flies that appeared in the second generation, low grade parents
were selected. These *at once* established a low grade race that gave
means constantly and unquestionably lower than the high selected race;
no variation in the environment was great enough to confuse them.
This low race did not show any signs of weakening on account of the
selection of low grade flies; it was continued for 19 generations and gave
large families. The reason for this is that all the flies, even the large
well fed ones, had fewer extra bristles than the flies in the uncrossed high
selected race; their germ plasm was different. It is very evident that
the results of this crossing can not be explained on the basis of non-
genetic physiological causes, as Castle[4] has suggested may explain the
very closely parallel results of his crosses with self-colored and hooded
rats. In spite of this recent interpretation, it is well to note that Castle
has given unmistakable evidence that his crosses involved genetic modi-

fication. By plus selection from hooded rats that came from a cross between the minus selected race and wild, the minus race was immediately transformed into the plus race, whereas similar plus selection from the minus race *without* the cross with wild, required 6 generations to move the means even up *to* the "0" grade.

There are then, four lines of evidence that support the conclusion that selection, in the case of extra bristles has separated genetic differences, or units, that existed at the beginning of the experiment, and that did not reappear *de novo:* (1) at first correlation coefficients are constantly positive and significant, later they are mainly not significant and fluctuate between positive and negative; (2) selection advances the means at first, later it does not; (3) before selection makes its advance, return, or low, selection separates a distinct race, while afterwards, the same procedure fails to accomplish the same result, however, (4) if a cross with normal precedes, the low selection becomes as effective as it was at the beginning.

As the material under discussion does not constitute a pure line in any sense, the conclusions drawn do not have any immediate bearing on the pure line theory. Moreover, environment plays such a conspicuous role that nothing positive can be said about any hypothetica variations in the germ plasm that may be hidden by variations in the environment, and accordingly be too small to be determinable. It may be suggested that if the environment were not such a controlling factor, or if it were possible to reduce the variability of the environment, smaller changes in the germ plasm might be discovered. This claim may be made for any work in selection that could be imagined; no failure of selection, however stationary the environment may seem to be, can escape this claim, namely that variations in the germ plasm may be taking place, although they are not distinguishable in the soma. The claim may be made, but it will give neither the breeder, nor natural selection any opportunity to make progress. It appears that instead of offering a fatal objection to the work here reported, the evident environmental factor serves well to emphasize the utter futility of attempting to deal in theory or fact with supposed germinal phenomena that can never be demonstrated or utilized. The variations in environment commensurate with the viability of the fly are great, but they do not hide the fact that there are germinal differences in regard to the numbers of extra bristles; they do not hide the fact that two races may be raised at the same time under the same conditions and maintain their individuality; nor do they explain the fact that after selection has made a certain amount of progress it is no longer possible to raise the means of

the race any further and no longer possible to separate two distinct races by selection without a cross with normal.

The conclusions that logically follow from the preceding discussion are that (1) extra bristles are primarily occasioned by one germinal unit and further influenced by other germinal units, and (2) that no change that could have either evolutionary or practical significance has occurred in these units during the 50 generations of the experiment.

[1] Pearl, R., *J. Exp. Zool., Philadelphia,* **13,** 1912, (283–394); Nilsson, Hj., see De Vries, *Plant Breeding;* De Vries, H., *The Mutation Theory;* Tower, W. L., *Washington, Pub. Carnegie Inst.,* No. 48; Johannsen, W., *Elemente der Exacten Erblichkeitslehre.*

[2] Castle, W. E., and Phillips, J. C., *Washington, Pub. Carnegie Inst.,* No. 195; Smith, L. H., *Univ. Ill. Agric. Exp. Sta. Bull.,* No. 128; Middleton, R., *J. Exp. Zool., Philadelphia,* **19,** (451–503); Jennings, H. S., *Genetics, Cambridge,* **1,** (407–534).

[3] MacDowell, E. C., *J. Exp. Zool., Philadelphia,* **19,** (61–98).

[4] Castle, W. E., and Wright, S., *Washington, Pub. Carnegie Inst.,* No. 241.

PRESSURE PHENOMENA ACCOMPANYING THE GROWTH OF CRYSTALS

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Under suitable conditions crystals grow in directions in which growth is opposed by external force. This fact appears to have been first observed by Lavalle in 1853.[1] It was denied, however by Kopp, who, after making certain experiments, stated that he was never able to observe anything tending to confirm the view that a crystal can raise itself in order to grow also on the side on which it rests.[2] Subsequently the observations of Lavalle were confirmed by Lehmann[3] and others.

Becker and Day seem to have made the first attempt at determining the magnitude of the force developed during crystal growth. In their experiment, a crystal of alum supporting a weight was covered with a saturated solution of alum, and supersaturation was induced by evaporation. The crystal increased in size through growth on the lateral exposed faces which were also extended downward, thus lifting the crystal together with its load. The deposition of new material on the lower surface was restricted to the periphery, so that a hollow face was gradually formed by the downward extension of the new growth, and the crystal rested on a very narrow outer rim. The area of this rim was determined with difficulty, but repeated measurements led to the conclusion that "the force per unit area which the crystals exert . . . .